

## Foraging Seabirds Respond To An Intermittent Meteorological Event In A Coastal Environment

Waggitt, James; Torres, Ricardo; Fraser, Shaun

### Marine Ornithology

Published: 15/04/2020

Peer reviewed version

[Cyswllt i'r cyhoeddiad / Link to publication](#)

*Dyfyniad o'r fersiwn a gyhoeddwyd / Citation for published version (APA):*

Waggitt, J., Torres, R., & Fraser, S. (2020). Foraging Seabirds Respond To An Intermittent Meteorological Event In A Coastal Environment. *Marine Ornithology*, 48(1), 123-131.

#### Hawliau Cyffredinol / General rights

Copyright and moral rights for the publications made accessible in the public portal are retained by the authors and/or other copyright owners and it is a condition of accessing publications that users recognise and abide by the legal requirements associated with these rights.

- Users may download and print one copy of any publication from the public portal for the purpose of private study or research.
- You may not further distribute the material or use it for any profit-making activity or commercial gain
- You may freely distribute the URL identifying the publication in the public portal ?

#### Take down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

# **Foraging Seabirds Respond To An Intermittent Meteorological Event In A Coastal Environment**

JAMES J.WAGGITT<sup>1</sup>, RICARDO TORRES<sup>2</sup>, SHAUN FRASER<sup>3</sup>

<sup>1</sup> *School of Ocean Sciences, Bangor University, Anglesey, UK, LL59 5AB*

<sup>2</sup> *Plymouth Marine Laboratory, Plymouth, UK, PL1 3DH*

<sup>3</sup> *NAFC Marine Centre, University of the Highlands and Islands, Shetland, UK, ZE1 0UN*

*Received 31 October 2019, accepted 18 February 2020*

## ABSTRACT

WAGGITT, J.J., TORRES, R. & FRASER, S. 2020. Foraging Seabirds Respond To An Intermittent Meteorological Event In A Coastal Environment. *Marine Ornithology*.

Temporal variations in the numbers of foraging seabirds usually coincide with concurrent variations in physical processes influencing prey availability. Responses to periodic tidal currents are commonly reported, with certain tidal states being favoured. By contrast, responses to intermittent meteorological events have rarely been reported, even though wind-driven exchanges of water masses or intrusion of estuarine plumes could have similar consequences. As large-scale offshore constructions (e.g. aquaculture, coastal defences, ports and marine renewable energy installations) and climate variations alter periodic tidal currents and intermittent meteorological events, respectively, quantifying responses to these physical processes identifies potential impacts on seabird communities. This study quantifies responses of foraging seabirds to physical processes in the Ria de Vigo, north-western Spain. The numbers of foraging European Shags *Phalacrocorax aristotellus* and Yellow-legged Gulls *Larus michahellis* showed no response to variations in current direction and speed. By contrast, both increased in number during an estuarine plume intrusion (the Western Iberian Buoyant Plume: WIBP) following an extreme river discharge event and southerly winds. These increases may be explained by the temporary combination of marine and brackishwater fauna, increasing prey biomass. The frequency of extreme river discharge events is likely to decrease in north-western Spain. If WIBP intrusions consistently enhance prey availability, observations of large numbers of foraging seabirds using the ria could become rarer.

**Key Words:** estuarine plume, foraging ecology, European Shag, *Larus michahellis*, *Phalacrocorax aristotellus*, vessel-based surveys, Yellow-legged Gull

## INTRODUCTION

For foraging seabirds, coastal environments represent important habitats due to physical processes that enhance prey availability (Cox *et al.* 2018). However, numerous physical processes in coastal environments are susceptible to anthropogenic-driven changes. Large-scale offshore constructions (e.g. aquaculture, coastal defences, ports and marine

renewable energy installations; Carter 2013) alter tidal currents (Cazenave *et al.* 2016, De Dominicis *et al.* 2017, Fraser *et al.* 2017, Shields *et al.* 2011) whereas climate change and oscillations (e.g. North Atlantic Oscillation, El Nino Southern Oscillation) alter meteorological events (Stenseth *et al.* 2003, Harley *et al.* 2006). Identifying the responses of foraging seabirds to tidal currents and meteorological events in coastal environments would highlight potential impacts of anthropogenic-driven changes.

In coastal environments, periodic changes in the direction/speed of tidal currents and depth across ebb-flood cycles are a conspicuous physical process (Simpson *et al.* 2012). These changes influence prey availability. For seabirds targeting pelagic prey, a certain current direction or speed could advect prey from productive neighbouring areas, increasing encounters with prey (Zamon 2001). In other cases, certain combinations of current direction/speed and topography create turbulent eddies and shear-lines, entraining and aggregating prey (Johnston *et al.* 2007). For seabirds targeting benthic prey, the energetic cost of dives is reduced at slow current speeds and shallow depths, increasing the accessibility of prey (Heath *et al.* 2010). Studies showing the number of foraging seabirds increasing during certain tidal states are numerous and widespread (Hunt *et al.* 1999, Benjamins *et al.* 2015; Waggitt *et al.* 2016a, 2016b).

In some coastal environments however, meteorological events (e.g. extreme river discharge or intense wind) also represent important physical processes. Estuarine plumes following extreme river discharge events alter salinity and temperature (Gillanders *et al.* 2002), whereas exchanges of water masses during intense wind events have similar effects (Kämpf *et al.* 2016). As with tidal currents, these meteorological events could also influence prey availability. For instance, onshore advection of productive water masses encourage prey to form denser schools (Benoit-Bird *et al.* 2019). Estuarine plumes encourage brackish-water species into the open-ocean, increasing prey biomass (Kingsford *et al.* 1994). The frequency of these meteorological events is usually seasonal, with the highest numbers of foraging seabirds seen when favourable meteorological events are most likely (Cox *et al.* 2018). However, the timing of individual meteorological events within seasons are intermittent and unpredictable. Studies showing changes in the number of foraging seabirds during an intermittent meteorological event are scarce (Cox *et al.* 2018).

This study compares responses of foraging seabirds to periodic tidal currents and an intermittent meteorological event in the Ria de Vigo, north-western Spain (42° 15' 04" N, 8° 53' 30" W) (Fig.1). During the study, an estuarine plume (the Western Iberian Buoyant Plume, WIBP; Sousa *et al.* 2014) originating from the Minho Estuary (Fig.1) entered the ria, following an extreme river discharge event and southerly winds. In the same area, tidal currents flow through a narrow (2.8 km) and shallow (~25 m) channel (Fig.1), causing periodic variation in their direction/speed. This study uses the co-occurrence of these tidal currents and the WIBP intrusion to ask whether: (1) temporal changes in the number of foraging seabirds are correlated to these physical processes, (2) the strength of correlations are greater for physical processes associated with tidal currents or the WIBP intrusion?

## METHODS

### Study Area

This study was conducted on seven days between 4 and 15 June 2018. This period coincided with the breeding seasons of the dominant seabird species in the ria: European Shag *Phalacrocorax aristotellis* and Yellow-legged Gull *Larus michahellis*. The study area covered approximately 48 km<sup>2</sup> in the northern ria (Fig.1). The latter encompasses sand-banks known to be exploited by shags and gulls feeding predominantly on sandeel *Ammodytidae* (Velando *et al.* 1999) and Henslow's swimming crab *Polybius henslowii* (Munilla 1997), respectively. The recording of temporal variations in the numbers of foraging seabirds and physical processes occurred exclusively within the study area.

### Seabird Abundance

A single observer recorded temporal variation in the number of foraging seabirds during 40 zig-zag transects of approximately 10.3 km in length (Fig. 1). Transects were performed from a rigid inflatable boat moving at an average speed of 14 kt (11.2 – 17 kt), and lasted an average of 23 min (19 – 30 min). The numbers of transects were spread relatively evenly between ebb ( $n = 19$ ) and flood ( $n = 21$ ) tides. Throughout the transects, the observer followed European Seabirds At Sea (ESAS) methodology (Tasker *et al.* 1984). However, the observer was only 1 m above sea-surface. To ensure that the observer recorded representative numbers of animals, transects were only performed when the sea state was less than Beaufort

Scale 3. Nevertheless, estimations of sea state were recorded at the start of each transect to account for possible changes in the detectability of animals during rough weather (Camphuysen *et al.* 2004). These estimations represented a mean across the study area, and included non-integer values if there were spatial variations in weather conditions. Animals seen diving, dip-feeding and searching were considered as foraging seabirds (Camphuysen *et al.* 2012). As transects were performed away from breeding colonies, animals sitting on the sea-surface were likely resting between foraging bouts rather than alongside nests (Waggitt *et al.* 2016a, 2016b), and were also considered as foraging seabirds. Yellow-legged Gulls seen scavenging around fishing vessels were not considered as foraging seabirds (Valeiras 2003).

## Physical Processes

Periodic tidal currents were quantified using outputs from an existing Finite Volume Community Ocean Model (FVCOM) (Chen *et al.* 2003) developed for the ria. Outputs were available at 15 min and approximately 100 m resolution. Mean depth averaged speed would summarise general conditions over the study area, whereas maximum or surface speeds may detect the presence or absence of strong hydrodynamic features at certain locations (Benjamins *et al.* 2015). Analyses was concerned with variations in the number of foraging seabirds across the study area, rather than associations between foraging seabirds and strong hydrodynamic features (e.g. Waggitt *et al.* 2016a). Therefore, for each transect, periodic tidal currents were represented by the mean depth averaged speed ( $\text{m s}^{-1}$ ) across the study area at the start of observations (Supplementary Material, S1). To discriminate between current directions, currents from the north were converted into negative values. Therefore, negative values show ebb currents, and positive values represent flood currents.

The WIBP intrusion was quantified using outputs from an existing Nucleus for European Modelling of the Ocean (NEMO) model (Madec 2008) developed for the Iberian region (Sotillo *et al.* 2015) (<http://marine.copernicus.eu>). Outputs were available at daily and 7 km resolution. For each transect, the influence of the WIBP was represented by the mean salinity (ppt) across the study area on the day of observations (Sousa *et al.* 2014). The arrival and departure of the WIBP intrusion in the study area would be identified by decreasing and increasing salinities, respectively. Data processing was performed in the ‘raster’ package (Hijmans 2013) in R (version 3.5.1, R Development Core Team 2018).

## Statistical Analysis

Generalised Additive Models (GAMs) identified and quantified correlations between the number of foraging seabirds and physical processes (Wood 2006). A negative binomial distribution was used to account for overdispersion in the number of seabirds. The response variable was the number of foraging seabirds seen per transect. The explanatory variables were the corresponding measurements of depth averaged current speed, salinity and sea state. Salinity and sea state were modelled as continuous and linear variables. Whilst sea state is sometimes modelled as a categorical variable, a general decrease in detectability with increasing sea state was expected, making a linear variable more appropriate. Depth averaged current speed was modelled as a continuous and non-linear variable, with the number of knots fixed at 3. This setup allowed relationships with maximum speed, maximum speed in a particular direction (south or north), and slack water to be detected. Salinity was modelled as a continuous and linear variable. Sea state was included to account for possible decreases in the detectability of foraging seabirds in rough weather (Camphuysen *et al.* 2004). GAM were constructed using the ‘mgcv’ package (Wood 2006) in R.

Backwards model-selection based on *p*-values was performed (Zuur *et al.* 2009). Residuals from resultant models showed no evidence of temporal autocorrelation (Supplementary Material S2). Predicted variances in the number of foraging seabirds across gradients in physical processes were calculated from model parameters. In these calculations, the physical process of interest was varied between its minimum and maximum value, whilst other physical processes were held at their mean values. The magnitude and strength of relationships between numbers of foraging seabirds and physical processes were quantified using proportional differences (*Pd*). *Pd* represented the absolute difference between the maximum and minimum predicted values divided by the minimum predicted value, allowing direct comparisons between physical processes (Waggitt *et al.* 2017, 2018). Model selection and prediction were performed using the ‘mgcv’ package in R.

## RESULTS

The WIBP intrusion originated from the Minho estuary following an extreme river discharge event on June 6. Southerly winds (see <https://www.meteogalicia.gal>) then advected the WIBP towards the study site between 7 and 9 June (Fig. 2). Decreasing salinities indicated the

arrival of the WIBP on June 10, with increasing salinities indicating its dispersal on June 12 (Fig. 3). Periodic tidal currents were considerably faster when flowing from the north than from the south, with rapid changes in direction seen at slack water (Fig. 3).

The mean daily count of foraging European Shags peaked at 64.8 on 11 June, coinciding with the WIBP intrusion (Fig.3). The highest count in one transect on 11 June was 100 animals. On the remaining six days, the daily mean count was considerably lower. However, counts were generally higher before 11 June (lowest = 15.3, highest = 22.6) than after (lowest = 4.7, highest = 16.5) (Fig.3). The decrease after 11 June coincided with higher occurrence of rough weather; 71% of transects experienced sea states greater than Beaufort Scale 1.5. Accordingly, European Shags showed negative relationships with salinity and sea state (Fig.4). No relationships were found with depth averaged current speed. When accounting for the effect of sea state, *Pd* values indicated that (on average) 3.6 times more European Shags were encountered during WIBP intrusions than typical scenarios (Fig.4).

The daily mean count of foraging Yellow-legged Gulls also peaked on 11 June (56.3), again coinciding with the WIBP intrusion (Fig.3). The highest count in one transect on 11 June was 94 animals. Daily mean counts after 11 June were comparable to those during the plume event (lowest = 34.3, highest = 44.6); those before were considerably lower (lowest = 9.0, highest = 16.5) (Fig.3). The former coincided with higher numbers of transects being performed in rough weather (see above) (Fig.3). Accordingly, Yellow-legged Gulls showed negative relationships with salinity, and positive relationships with sea state (Fig.4). No relationships were found with depth averaged current speed. When accounting for the effect of sea state, *Pd* values indicated that (on average) 4.2 times more Yellow-legged Gulls were encountered during WIBP intrusions than typical scenarios (Fig.4).

## DISCUSSION

This study quantified the influence of periodic tidal currents and an intermittent meteorological event on the number of foraging seabirds in the Ria de Vigo in north-western Spain. Foraging European Shags and Yellow-legged Gulls showed no responses to periodic tidal currents. By contrast, numbers of both species increased during a WIBP intrusion on 11 June. The numbers of foraging seabirds were also correlated to measurements of sea state.



The discussion focusses on responses of foraging seabirds to periodic tidal currents, intermittent meteorological events, and comparisons between these physical processes. The potential impacts from anthropogenic-driven changes within the ria are also discussed.

### **Periodic Tidal Currents**

Increases in the numbers of foraging seabirds during certain tidal states are commonplace in areas of both strong ( $> 1 \text{ m s}^{-1}$ ) (Benjamins *et al.* 2015) and weak currents ( $< 0.5 \text{ m s}^{-1}$ ) (Embling *et al.* 2012, Scott *et al.* 2013). The absence of responses to periodic tidal currents in the ria suggests that the amount of prey advected from surrounding areas is consistent across tidal states and/or turbulent eddies and shear-lines emerging during certain tidal states do not increase prey availability. Alternatively, limited numbers of surveys across different tidal states and/or strong responses of foraging seabirds to the WIBP intrusion could prevent responses to periodic tidal currents being detected. Extending studies over longer periods could investigate these possibilities further by increasing the number of surveys performed across different tidal states and outside WIBP intrusions. In any case, this study shows that strong tidal patterns in numbers of foraging seabirds cannot be assumed in coastal environments, even though they represent a conspicuous physical process.

### **Intermittent Metrological Events**

Increased numbers of foraging seabirds in areas and seasons of persistent estuarine plumes are commonly reported (Cox *et al.* 2018). However, evidence of responses to an individual estuarine plume intrusion are scarce (Cox *et al.* 2018). As with previous examples, increases in the numbers of foraging seabirds during the WIBP intrusion are presumably explained by higher prey biomass. Local Yellow-legged Gulls forage primarily on Henslow's swimming crab (Munilla 1997). This detritivorous crab benefits from terrestrial-matter entering the water column (Vinagre *et al.* 2012), and observers noted Yellow-legged Gulls catching swarming crabs at the water surface. Whilst local European Shags forage consistently on sandeel, they sometimes exploit sand smelt *Atherina presbyter* in large numbers (Velando *et al.* 1999). This brackish-water fish (Wheeler 1969) is locally abundant, and it is speculated that European Shags exploited schools moving into the ria. However, whilst WIBP intrusions are commonplace in the ria (Des *et al.* 2019), studies over longer periods are needed to determine if responses occur during all WIBP intrusions.

Sea state is usually included in analyses to account for decreased detectability of animals during rough weather (Camphuysen *et al.* 2004). As expected, observers detected fewer European Shag in higher measurements of sea state. However, they detected more Yellowlegged Gull under the same circumstances. This could still indicate variation in detectability. The authors observed that Yellow-legged Gulls became restless during rough seas, and the tendency to take-off and land frequently could increase their detectability. However, it could also indicate differences in behaviour. European Shags detect and capture prey on the seabed using pursuit-dives. Therefore, European Shags may remain onshore during rough weather due to increased dive costs (Daunt *et al.* 2006, Lewis *et al.* 2015). By contrast, Yellow-legged Gulls detect and capture prey at the sea surface using dip-feeding or pecking. Animals could benefit from rough weather due to decreased flight costs (Haney *et al.* 1994) and resuspension of sub-surface material (Simpson *et al.* 2012). Therefore, relationships with sea state could be explained by both detectability and behaviour.

## Comparisons

Periodic tidal currents are known to influence prey availability, initiating responses by foraging seabirds (Hunt *et al.* 1999, Benjamins *et al.* 2015). However, this study shows that an intermittent meteorological event can cause stronger responses in some circumstances. These two processes almost certainly function synergistically, with numbers of foraging seabirds responding to the resultant conditions. Nevertheless, the relative influence of periodic tidal currents and intermittent meteorological events may relate to their control on conditions at a location. For instance, foraging Black-legged Kittiwakes *Rissa tridactyla* showed a greater response to periodic tidal currents in locations where current speeds were stronger (Trevail *et al.* 2019). Whilst the speed of periodic tidal currents cannot be considered weak in the ria, intermittent meteorological events have a much greater control on conditions in this area (Aristegui *et al.* 2006). This study suggests that the dynamics of foraging seabirds are intrinsically linked to that of the dominant process at a location.

## Anthropogenic Impacts

The frequency of extreme river discharge events is likely to decrease in north-western Spain

(Cardosa Pereira *et al.* 2019). Studies over longer periods are needed to investigate responses to periodic tidal currents better, and whether responses to WIBP intrusions are commonplace. However, if WIBP intrusions consistently enhance prey availability, then observations of large numbers of foraging seabirds using the ria could become rarer. Moreover, if animals breeding/roosting in the ria depend on occasional WIBP intrusions for their subsistence, they could suffer from decreased prey encounters and increased searching efforts. This study shows that investigating responses to periodic tidal currents and intermittent meteorological events identifies potential impacts from anthropogenic-driven changes in coastal environments.

## ACKNOWLEDGEMENTS

Surveys were funded by the NERC/DEFRA Marine Ecosystems Research Programme (NE/L003201/1) and the EU H2020 research and innovation programme (Grant agreement No 730984, ASSEMBLE Plus). We thank Antonio Villanueva, Jose Fernandez, Enrique Poza, Roberto Gómez and Alberto Velando for their assistance. We appreciate the time taken by an anonymous reviewer to provide helpful comments to improve our paper.

## REFERENCES

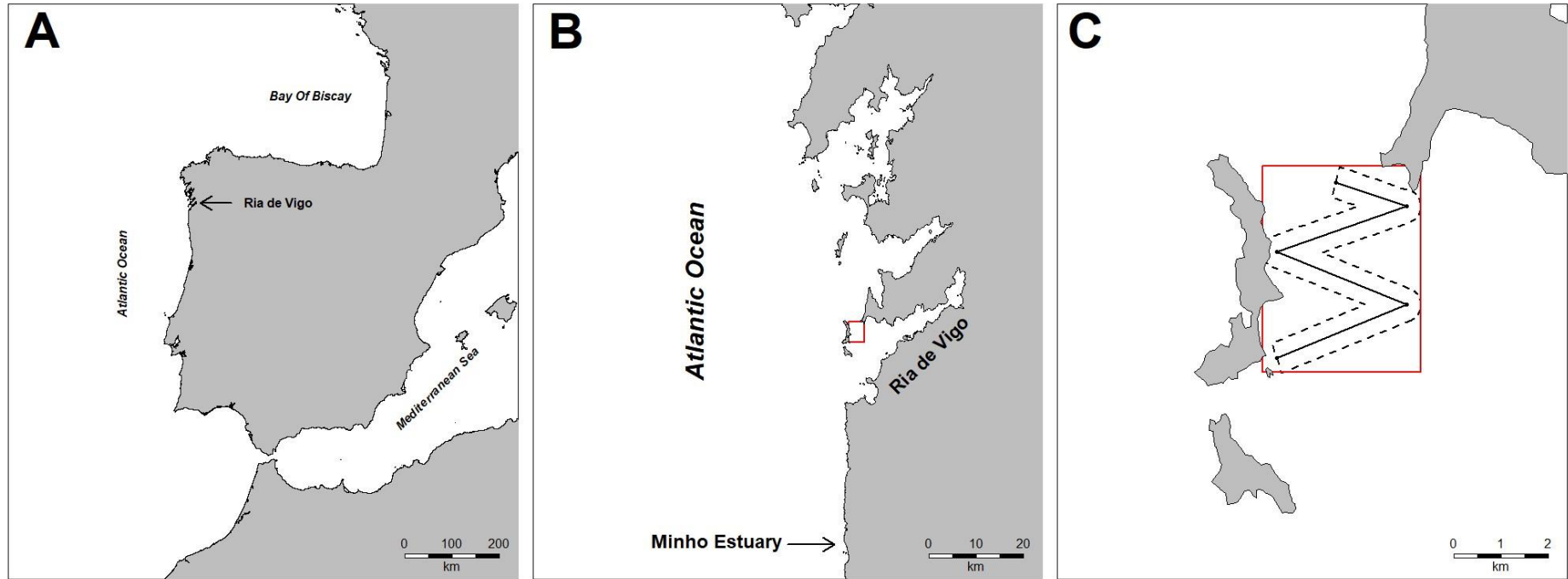
- ARISTEGUI, J., ÁLVAREZ-SALGADO, X.A., BARTON, E.D., FIGUEIRAS, F.G., HERNÁNDEZ-LEÓN, S., ROY, C. ET AL. 2006. Oceanography and fisheries of the Canary Current Iberian region of the Eastern North Atlantic. In: BRINK, K.H & ROBINSON, A.R. (Eds.). *The Global Coastal Ocean: Interdisciplinary Regional Studies and Syntheses*. Cambridge, MA: Harvard University Press, Vol. 14, pp. 877–931.
- BENJAMINS, S., DALE, A., HASTIE, G., LEA, M., SCOTT, B. E., WAGGITT, J. J. ET AL. 2015. Confusion reigns? A review of marine megafauna interactions with energetic tidal features. *Oceanography and Marine Biology: An Annual Review* 53:1–54.
- BENOIT-BIRD, K. J., WALUK, C. M. & RYAN, J. P. 2019. Forage Species Swarm in Response to Coastal Upwelling. *Geophysical Research Letters* 46:1537–1546.
- CAMPHUYSEN, C. J., FOX, A. D., LEOPOLD, M. F. & PETERSEN, I. K. 2004. *Towards standardised seabirds at sea census techniques in connection with environmental*

- 303 *impact assessments for offshore wind farms in the U.K.* Report by Royal Netherlands  
 304 Institute for Sea Research and the Danish National Environmental Research Institute.
- 305 CAMPHUYSEN, C. J., SHAMOUN-BARANES, J., BOUTEN, W. & GARTHE, S. 2012.  
 306 Identifying ecologically important marine areas for seabirds using behavioural  
 307 information in combination with distribution patterns. *Biological Conservation* 156:22–  
 308 29.
- 309 CARDOSO PEREIRA, S., MARTA-ALMEIDA, M., CARVALHO, A.C. & ROCHA, A.  
 310 2019. Extreme precipitation events under climate change in the Iberian Peninsula.  
 311 *International Journal of Climatology* 40: 1255-1278
- 312 CARTER, R., 2013. *Coastal Environments: An Introduction to the Physical, Ecological and*  
 313 *Cultural Systems of Coastlines*. London, UK: Academic Press.
- 314 CAZENAVE, P. W., TORRES, R. & ALLEN, J. I. 2016. Unstructured grid modelling of  
 315 offshore wind farm impacts on seasonally stratified shelf seas. *Progress in*  
 316 *Oceanography* 145:25–41.
- 317 CHEN, C., LIU, H. & BEARDSLEY, R. C. 2003. An Unstructured Grid, Finite-Volume,  
 318 Three-Dimensional, Primitive Equations Ocean Model: Application to Coastal Ocean  
 319 and Estuaries. *Journal of Atmospheric and Oceanic Technology* 20:159–186.
- 320 COX, S. L., EMBLING, C. B., HOSEGOOD, P. J., VOTIER, S. C. & INGRAM, S. N. 2018.  
 321 Oceanographic drivers of marine mammal and seabird habitat-use across shelf-seas: A  
 322 guide to key features and recommendations for future research and conservation  
 323 management. *Estuarine, Coastal and Shelf Science* 212:294–310.
- 324 DAUNT, F., AFANASYEV, V., SILK, J. R. D. & WANLESS, S. 2006. Extrinsic and  
 325 intrinsic determinants of winter foraging and breeding phenology in a temperate  
 326 seabird. *Behavioural Ecology and Sociobiology* 59:381–388.
- 327 DE DOMINICIS, M., O'HARA MURRAY, R. & WOLF, J. 2017. Multi-scale ocean  
 328 response to a large tidal stream turbine array. *Renewable Energy* 114:1160–1179.
- 329 DES, M., DECASTRO, M., SOUSA, M. C., DIAS, J. M. & GÓMEZ-GESTEIRA, M. 2019.  
 330 Hydrodynamics of river plume intrusion into an adjacent estuary: The Minho River and  
 331 Ria de Vigo. *Journal of Marine Systems* 189:87–97.
- 332 EMBLING, C. B., ILLIAN, J., ARMSTRONG, E., VAN DER KOOIJ, J., SHARPLES, J.,  
 333 CAMPHUYSEN, C. J. ET AL. 2012. Investigating fine scale spatio-temporal  
 334 predatorprey patterns in dynamic marine ecosystems: a functional data analysis  
 335 approach.

- 336 *Journal of Applied Ecology* 49:481–492.
- 337 FRASER, S. J., NIKORA, V., WILLIAMSON, B. J. & SCOTT B. E. 2017. Hydrodynamic  
338 impacts of a marine renewable energy installation on the benthic boundary layer in a  
339 tidal channel. *Energy Procedia* 125:250–259.
- 340 GILLANDERS, B.M. & KINGSFORD, M. J. 2002. Impact of changes in flow of freshwater  
341 on estuarine and open coastal habitats and the associated organisms. *Oceanography and*  
342 *Marine Biology: An Annual Review* 40:233:309.
- 343 HANEY, J. C. & LEE, D. S. 1994. Air-Sea Heat Flux, Ocean Wind Fields, and Offshore  
344 Dispersal of Gulls. *The Auk* 111:427–440.
- 345 HARLEY, C. D. G., HUGHES, A.R., HULTGREN, K. M., MINER, B. G., SORTE, C. J. B.,  
346 THORNBUR, C. S. ET AL. 2006. The impacts of climate change in coastal marine  
347 systems. *Ecology Letters* 9:228–241.
- 348 HEATH, J. P. & GILCHRIST, H. G. 2010. When foraging becomes unprofitable: energetics  
349 of diving in tidal currents by common eiders wintering in the Arctic. *Marine Ecology*  
350 *Progress Series* 403:279–290.
- 351 HIJMANS, R.J. 2017. *Raster: Geographic Data Analysis and Modelling*. R package version  
352 2.1-66. Retrieved from <http://CRAN.R-project.org/package=raster>.
- 353 HUNT, G. L., MEHLUM, F., RUSSELL, R. W., IRONS, D., DECKER, M. B. & BECKER,  
354 P. H. 1999. Physical processes, prey abundance, and the foraging ecology of seabirds.  
355 *International Ornithological Congress* 22: 2040–2056.
- 356 JOHNSTON, D. W. & READ, A. J. 2007. Flow-field observations of a tidally driven island  
357 wake used by marine mammals in the Bay of Fundy, Canada. *Fisheries Oceanography*  
358 16:422–435.
- 359 KÄMPF, J. & CHAPMAN, P. 2016. *Upwelling Systems of the World*. Springer International  
360 Publishing, Switzerland.
- 361 KINGSFORD, M. J. & SUTHERS, I. M. 1994. Dynamic estuarine plumes and fronts:  
362 importance to small fish and plankton in coastal waters of NSW, Australia. *Continental*  
363 *Shelf Research* 14:655–672.
- 364 LEWIS, S., PHILLIPS, R. A., BURTHE, S. J., WANLESS, S. & DAUNT, F. 2015.  
365 Contrasting responses of male and female foraging effort to year-round wind  
366 conditions. *Journal of Animal Ecology* 84:1490–1496.
- 367 MADEC, G. 2008. *NEMO Ocean General Circulation Model. Reference Manual*. Report by  
368 Laboratoire d'Océanographie Dynamique et de Climatologie.

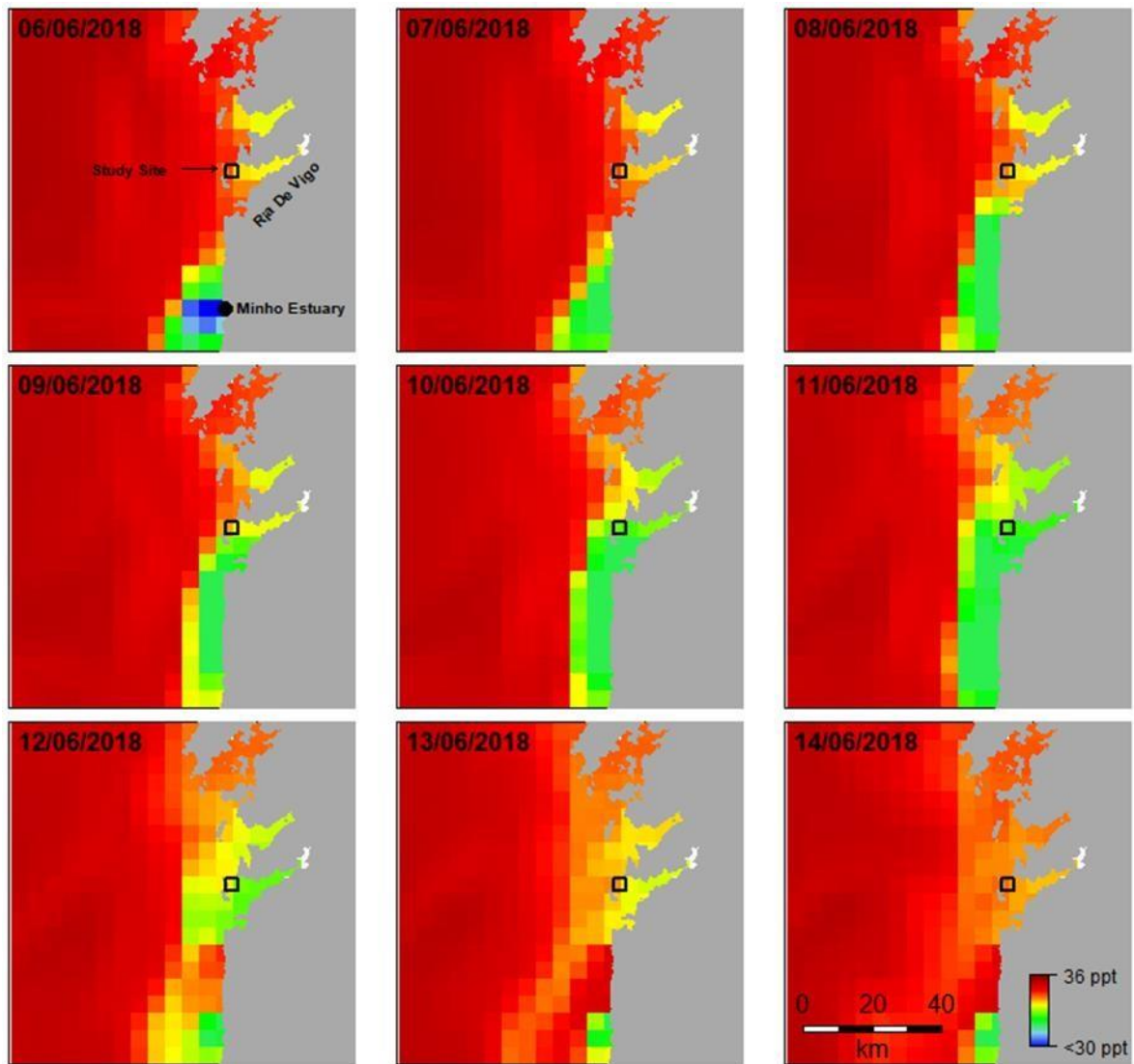
- MUNILLA, I. 1997. Henslow's swimming crab (*Polybius henslowii*) as an important food for yellow-legged gulls (*Larus cachinnans*) in NW Spain. *ICES Journal of Marine Science* 54:631–634.
- SCOTT, B. E., WEBB, A., PALMER, M. R., EMBLING, C. B. & SHARPLES, J. 2013. Fine scale bio-physical oceanographic characteristics predict the foraging occurrence of contrasting seabird species; Gannet (*Morus bassanus*) and storm petrel (*Hydrobates pelagicus*). *Progress in Oceanography* 117:118–129.
- SHIELDS, M. A., WOOLF, D. K., GRIST, E. P. M., KERR, S. A., JACKSON, A. C., HARRIS, R. E. ET AL. 2011. Marine renewable energy: The ecological implications of altering the hydrodynamics of the marine environment. *Ocean and Coastal Management* 54:2–9.
- SIMPSON, J. H. & SHARPLES, J. 2012. *Introduction to the Physical and Biological Oceanography of Shelf Seas*. Cambridge, UK: Cambridge University Press.
- SOTILLO, M. G., CAILLEAU, S., LORENTE, P., LEVIER, B., AZNAR, R., REFFRAY, G. ET AL. 2015. The MyOcean IBI Ocean Forecast and Reanalysis Systems: operational products and roadmap to the future Copernicus Service. *Journal of Operational Oceanography* 8:63–79.
- SOUSA, M. C., VAZ, N., ALVAREZ, I., GOMEZ-GESTEIRA, M. & DIAS, J. M. 2014. Influence of the Minho River plume on the Rias Baixas (NW of the Iberian Peninsula). *Journal of Marine Systems* 139:248–260.
- STENSETH, N. C., OTTERSEN, G., HURRELL, J. W., MYSTERUD, A., LIMA, M., CHAN, K. ET AL. 2003. Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 270:2087–2096.
- TASKER, M. L., JONES, P. H., DIXON, T.J. & BLAKE, B. F. 1984. Counting seabirds at sea from ships: a review of methods employed and a suggestion for a standardized approach. *The Auk* 101:567–577.
- TREVAIL, A. M., GREEN, J. A., SHARPLES, J., POLTON, J. A., ARNOULD, J. P. Y. & PATRICK, S. C. 2019. Environmental heterogeneity amplifies behavioural response to a temporal cycle. *Oikos* 128:517–528.
- VALEIRAS, J. 2003. Attendance of scavenging seabirds at trawler discards off Galicia, Spain. *Scientia Marina* 67:77–82.

- 402 VELANDO, A. & FREIRE, J. 1999. Intercolony and seasonal differences in the breeding diet  
403 of European shags on the Galician coast (NW Spain). *Marine Ecology Progress Series*  
404 188:225–236.
- 405 VELANDO, A. & MUNILLA, I. 2008. *Plan de Conservacion del Cormoran Monudo en el*  
406 *Parque Nacional de las Islas Atlanticas*. Vigo. Report by Universidade de Vigo.
- 407 VINAGRE, C., MÁGUAS, C., CABRAL, H. N. & COSTA, M. J. 2012. Food web structure  
408 of the coastal area adjacent to the Tagus estuary revealed by stable isotope analysis.  
409 *Journal of Sea Research* 67:21–26.
- 410 WAGGITT, J. J., CAZENAVE, P. W., TORRES, R., WILLIAMSON, B. J. & SCOTT, B. E.  
411 2016a. Quantifying pursuit-diving seabirds' associations with fine-scale physical  
412 features in tidal stream environments. *Journal of Applied Ecology* 53:1653–1666.
- 413 WAGGITT, J. J., CAZENAVE, P., TORRES, R., WILLIAMSON, B. J. & SCOTT, B. E.  
414 2016b. Predictable hydrodynamic conditions explain temporal variations in the density  
415 of benthic foraging seabirds in a tidal stream environment. *ICES Journal of Marine*  
416 *Science* 73:2677–2686.
- 417 WAGGITT, J. J., ROBBINS, A. M. C., WADE, H. M., MASDEN, E. A., FURNESS, R. W.,  
418 JACKSON, A. C. ET AL. 2017. Comparative studies reveal variability in the use of  
419 tidal stream environments by seabirds. *Marine Policy* 81:143–152.
- 420 WAGGITT, J. J., DUNN, H. K., EVANS, P. G. H., HIDDINK, J. G., HOLMES, L. J.,  
421 KEEN, E. ET AL. 2018. Regional-scale patterns in harbour porpoise occupancy of tidal  
422 stream environments. *ICES Journal of Marine Science* 75: 701–710.
- 423 WHEELER, A., 1969. *The Fishes of the British Isles and North West Europe*. London, UK:  
424 MacMillan.
- 425 WOOD, S. N., 2006. *Generalized Additive Models: An Introduction with R*. Boca Raton, LA:  
426 Chapman and Hall/CRC Press.
- 427 ZAMON, J. E., 2001. Seal predation on salmon and forage fish schools as a function of tidal  
428 currents in the San Juan Islands, Washington, USA. *Fisheries Oceanography* 10:353–  
429 366.
- 430 ZUUR, A. F., IENO, E. N., WALKER, N., SAVELIEV, A. A. & SMITH, G. M. 2009. *Mixed*  
431 *Effects Models and Extensions in Ecology with R*. New York, NY: Springer.

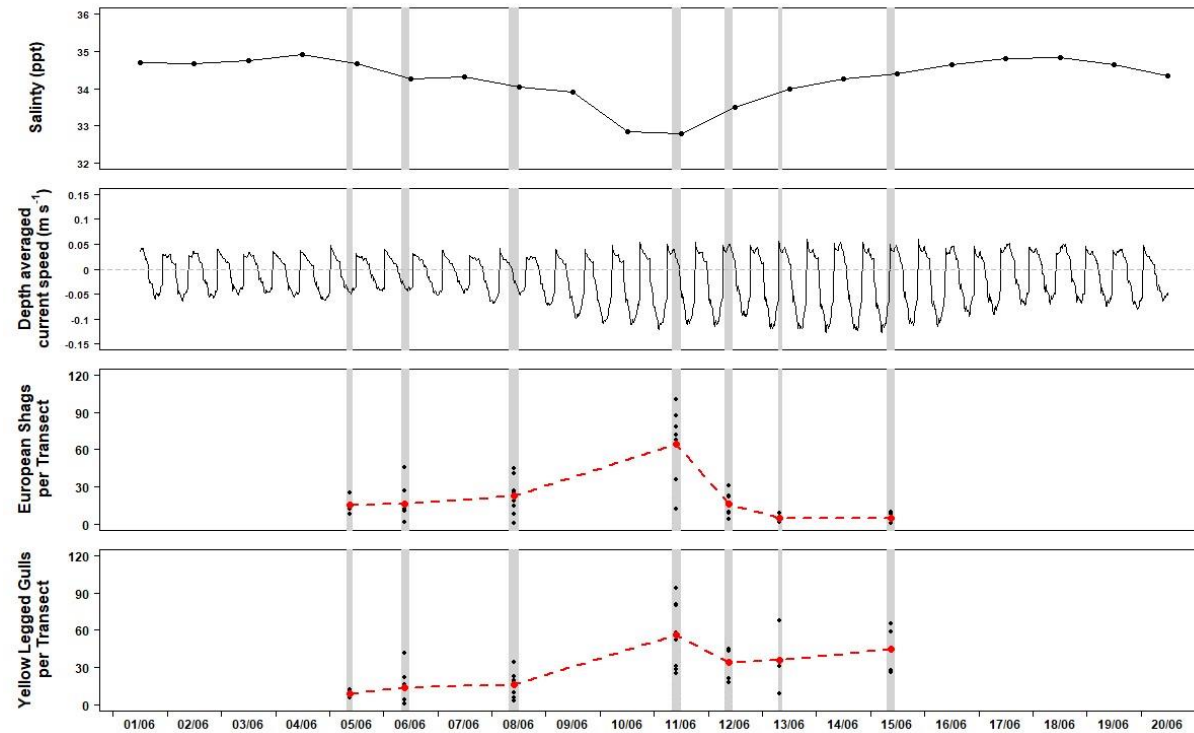


**Fig 1:** (A) The location of the Ria de Vigo in north-western Spain, (B) the area surrounding the ria, and (C) the zig-zag transects (solid black line) and observation area (dashed line) used to count numbers of foraging seabirds. The study area is shown by a red box.

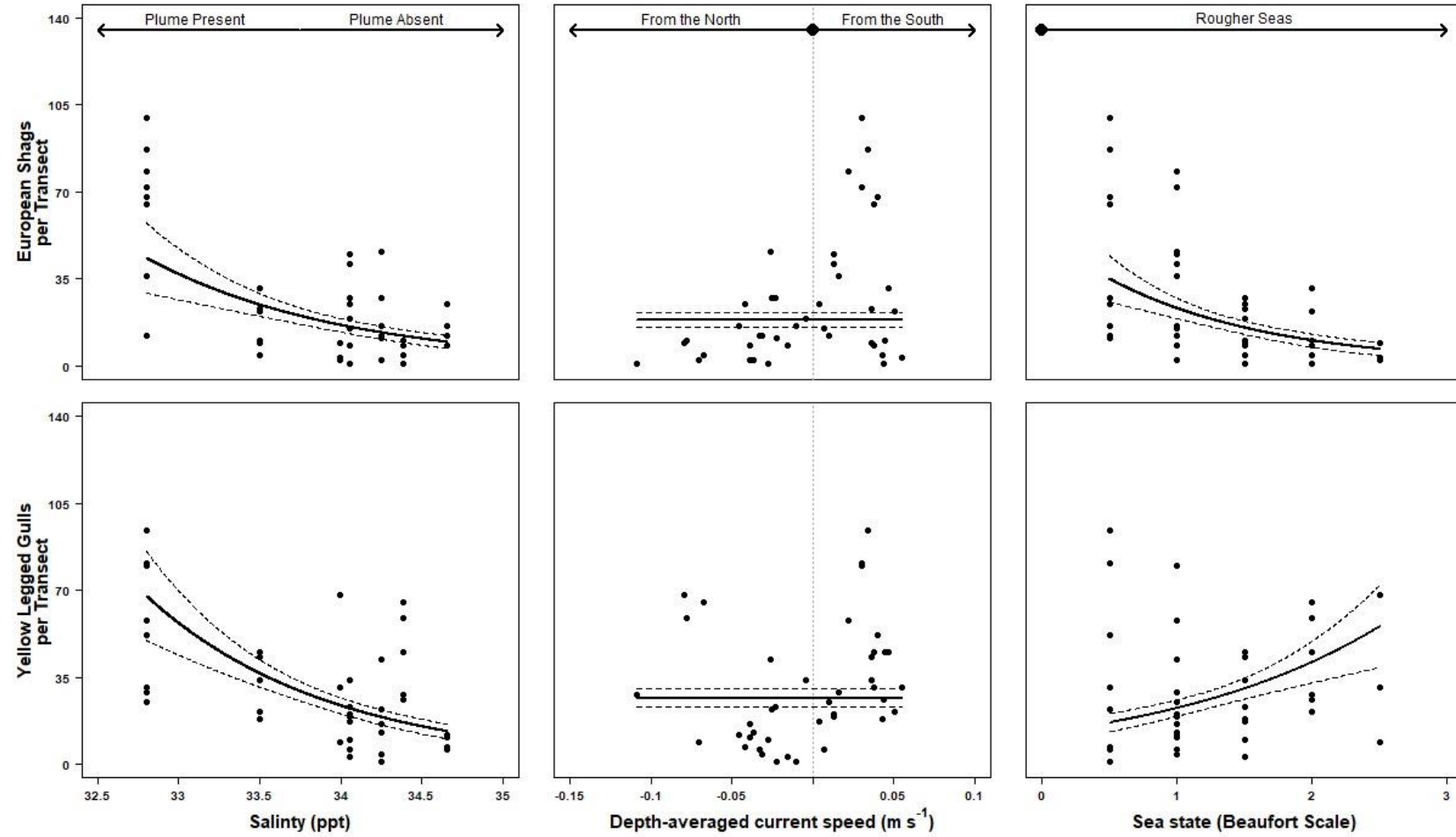




**Fig 2:** Variations in salinity between 6 and 14 June 2018 in the Ria de Vigo and the area surrounding the ria in north-western Spain. Values were sourced from an existing Nucleus for European Modelling of the Ocean (NEMO) model (Madec 2008) developed for the Iberian region (Sotillo *et al.* 2015). The study area is shown by a black box.



**Fig 3:** Temporal variations in salinity (ppt), depth-averaged tidal current speed ( $\text{m s}^{-1}$ ) and numbers of foraging seabirds during June 2018 in the Ria de Vigo, north-western Spain. Values of salinity were sourced from an existing Nucleus for European Modelling of the Ocean (NEMO) model (Madec 2008) developed for the Iberian region (Sotillo *et al.* 2015). Values of depth-averaged tidal current speeds were sourced from an existing FVCOM (Chen *et al.* 2003) developed for the ria. Negative values of depth-averaged tidal current speed represent flows from the north, whereas positive values represent flows from the south. Grey bars indicate times of zig-zag transects recording the numbers of foraging seabirds. Black points represent individual counts of foraging seabirds from zig-zag transects. Red points and lines illustrate daily mean counts of foraging seabirds among zig-zag transects.



**Fig 4:** Predicted variations ( $\pm$  standard error) in counts of foraging seabirds across different physical conditions from 4 to 15 June in the Ria de Vigo, north-western Spain. Predictions were made using generalized additive models (GAM) with a negative binomial distribution.